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# RESULTS OF HYBRIDIZING RING-DOVES, INCLUDING SEX-LINKED INHERITANCE.

BY R. M. STRONG.

## I. INTRODUCTION.

The work which is described in this paper was undertaken at the suggestion of the late Professor Whitman. It was begun in a small way during the spring of 1904 and it was continued during the years from 1905 to 1909 with the hope that opportunities for more extensive breeding experiments might appear later. During the year 1910 it was decided to discontinue the work because there was still no prospect in sight of a suitable plant for the breeding of birds on a scale sufficiently large for overcoming difficulties which appeared in the course of the work and which will be noted in this paper.

Two preliminary statements concerning this work have been published (Strong, '11 and '12).

Some statements concerning the care of the birds employed and their breeding habits have been included with the hope that they may be of value to other breeders of birds.

Professor Whitman housed portions or all of the stock during several winters, and invaluable suggestions were received from him concerning the care of the doves and methods of book-keeping. He also furnished some of the stock which was difficult to obtain in the market.

Because of limited cage space Professor Whitman never tried to breed for statistical results. When the newly discovered Mendel's law came into prominence, it naturally received considerable attention from him. Though always critical of Mendelianism, he nevertheless admitted that he had observed phenomena which, at one time, before Mendel's law came to the attention of biologists, seemed to suggest conclusions similar to those of Mendel. However, the apparent absence of character segregations, usually, in the numerous crosses between species

as well as varieties of pigeons, which Professor Whitman obtained, did not encourage the growth of Mendelian ideas. Furthermore, his experience was largely with  $F_1$  hybrids as has been the case with other workers in crossing species of birds. Though sceptical of the importance of Mendel's law, he thought it worth while to make a test of it with birds.

Professor Whitman was profoundly impressed with the importance of ancestry and pureness of stock in breeding experi-

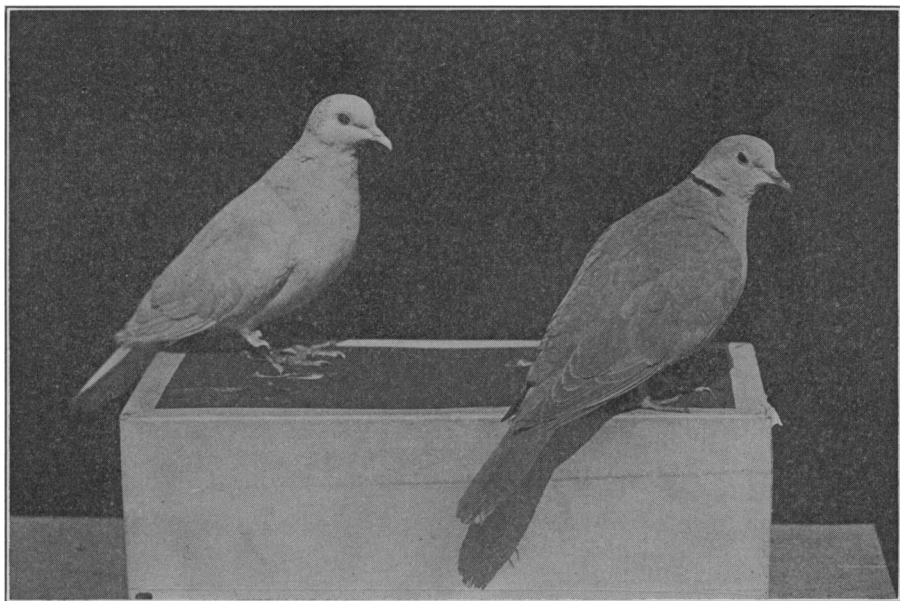


FIG. 1. From a photograph of a male white ring-dove and a female blond ring-dove. The sexes are alike, and hybrids between the blond and white ring-doves are practically not distinguishable from the above. This picture may be used consequently to represent both "pure" and hybrid birds of either sex.

ments. As domestic races of animals did not satisfy his ideals in these respects, he naturally turned to wild species for material. Unfortunately for statistical work, wild species do not breed freely in captivity, and hybrids are obtained with difficulty. Standing in a sense between wild species and domestic races of birds in breeding possibilities are the tame ring-doves which are commonly kept in cages. Professor Whitman had found

hybrids between the dark or blond ring-dove and the white ring-dove suggesting Mendelian phenomena (see Fig. 1). These birds breed true to type when not crossed, and they have a very simple color pattern. They do well in cages. Variations are so small that a very careful examination under very favorable conditions is required to distinguish individuals.

According to Salvadori ('93), the tame ring-doves are of unknown ancestry, but the dark form is referred to the species *Turtur risorius*, sub-genus *Streptopelia*. In Sharpe's Handlist (Sharpe, '99, p. 78) the term *Streptopelia risoria* Linn. is employed.

Salvadori ('93, p. 415) considered the white ring-dove, *Turtur alba*, to be a white variety of *Turtur risorius*, though he mentions the fact that Temminck and others have regarded the white bird as a distinct species. Whether the white and the blond ring-doves are to be regarded as different species must of course depend on the criterion employed. If the inter-breeding test which is involved in the code of the American Ornithologists' Union is applied, they cannot be called distinct species as they cross freely when together. However, Professor Whitman and others have produced many hybrids between species of doves often very distantly related. Only the freedom with which mating occurs and the apparently perfect fertility of the hybrids can be cited as distinguishing these ring-dove crosses from those between distinct species. The white ring-dove differs from the blond form chiefly in lacking the pigmentation of the latter. The blond bird has a dark bill which is about the color designated by No. 25 in the "Code des Couleurs" of Klinkensiek et Valette ('08). The beak of the white bird has a very light flesh-colored tint and is about 071 in the system just mentioned. Both have red feet about 17 in color. The skin of the blond bird is darker than that of the white bird.

Except for the black neck-ring, the predominating colors of the blond dove are fairly well indicated as lying between No. 103A and 103C (see Sharpe, '93, for a detailed description). For practical purposes in this paper, it is sufficient to describe the color of the blond ring-dove plumage as due to a dilute melanin pigmentation. Relatively small numbers of chromatophores

appear in the feather germs, and they resemble early stages in the development of the chromatophores which are found in the feather germs of most birds, except that they possess pigment distributing processes. Relatively small and light-colored melanin granules are formed. It is the intention of the writer to discuss these chromatophores more fully in another paper.

Minute traces of pigment are usually to be found in the plumage of the white bird, especially in the rectrices, but the feathers are practically pure white.

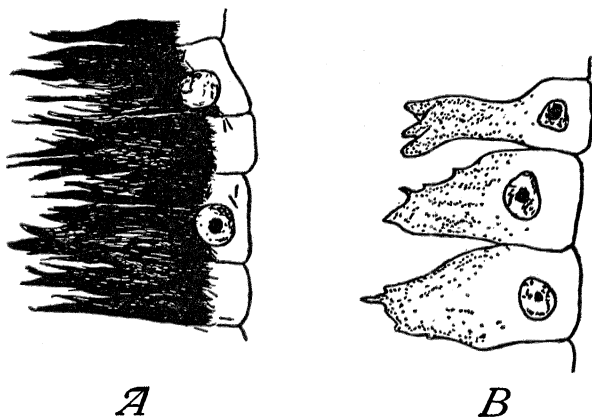


FIG. 2. Cells from the pigment epithelium of the retina,  $\times 1000$ . The birds were in strong diffused sunlight when killed so that the light condition existed. *A*, blond ring-dove cells; *B*, white ring-dove cells. The peculiar form of the cell processes seems to have been due to the shrinking of the pigment epithelium from the rods and cones layer in the preparations of white ring-dove eyes used for drawing.

The exposed portions of the eyes as seen in the live bird do not differ much in their general appearance for the two forms. An examination of the entire eye removed from its orbit, however, reveals a great difference in pigmentation. The eye of the white bird shows dark pigment in the iris region only, whereas the whole eye ball is dark in the case of the blond bird. A histological comparison was made with the following results. Spherical granules of what appears to be so-called melanin pigment occur in the iris of both birds in considerable quantities so that this region has a black appearance in fixed preparations. These granules vary greatly in size, the largest being about .0005 mm.

in diameter. Most of the granules are smaller than this. The choroid layer in the eye of the blond bird contains large amounts of the same pigment. Only minute traces of pigment occur in the choroid layer of the white ring-dove, and they are found with difficulty. This pigment appears to be the same as that found in the choroid of the blond bird except for its scarcity.

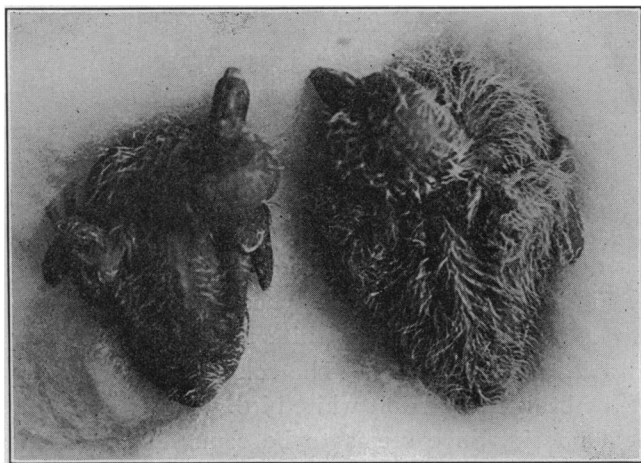


FIG. 3. From photograph of two nestling  $F_1$  hybrids. The smaller bird is two days old, and the larger, three days. The larger bird hatched from the first egg laid, and the smaller from the second egg in the same brood. The contrast in size is largely, if not entirely, due to the difference in age. The larger bird appears exactly like nestlings of pure blond ring-doves of the same age, and the smaller like those of the white ring-dove. The picture fails to show the great contrast in skin color which these birds exhibit at this stage. The smaller bird is very much lighter in color than the blond form, but the photograph failed to show this because the color of the skin has little actinic value.

The pigment epithelium in the eye of the blond bird is richly supplied with slender rod-shaped granules of melanin pigment (see Fig. 2, A). These granules are similar in appearance to those which are seen in the feathers of many birds but they differ from those of the ring-dove feather. In the white bird the pigment epithelium of the retina is almost devoid of pigment. A very pale brownish tint is sometimes given to the cell as seen under a high power objective, which is produced by extremely minute granules of what appears to be melanin pigment (see Fig.

2, B). These were observed with difficulty when a 1.5 mm. oil immersion objective and a No. 6 Zeiss ocular were employed. The microscopic picture which one of these pigment epithelium cells in the eye of the white bird presents, so far as its contained pigment is concerned, suggests strongly the appearance of a developing feather-germ chromatophore in a very early stage when pigment first appears. Various stages in the development of feather-germ chromatophores are figured by me in another paper (Strong, '02, Plate 6, note Fig. 30, especially).

The nestlings are decidedly different, even at hatching (see Fig. 3). It will be noticed that the down plumage of the white bird is much scantier than that of the blond dove nestling, and it is also somewhat whiter than the yellowish-white down of the blond nestling. The skin color is very different, though the contrast does not appear in the photograph which was used for making Fig. 3. The blond nestling has a rather dark skin which is about No. 93, whereas the white nestling has a light flesh-colored skin about No. 53C. The color of the latter is about that of the beak of the adult white bird.

The blond ring-dove seems to be somewhat more vigorous than the white ring-dove, and its voice is stronger. Professor Whitman was especially impressed with these points of difference. Unfortunately, no precise data for a comparison of the relative vigor of the two forms are at hand, and the above statements are based mostly on general impressions. The comparison for voice is easier to make as this is distinctly different in the two birds.

Melanin pigment appears in the iris region earlier in the blond nestlings than in the white birds. Thus, when the eyes have just become fully open, about one week after hatching, the whole visible eye in the live blond bird appears black. The white ring-dove nestling, on the other hand, shows only a dusky ring about the pupil, and a considerable amount of the eye still appears pink. This phenomenon will be referred to again in connection with the discussion of the observations which have been made by Miss Durham on canaries.

White ring-dove stock is not easy to obtain, and the birds are expensive. It is a curious fact that I found it hard to get female white ring-doves. Some of the stock both of blonds and of whites was imported.

## II. METHODS AND NOTES ON BREEDING HABITS.

Mating was accomplished usually by placing birds to be crossed in adjoining cages where other doves could not be seen. Visual impressions seem to be the significant factors in the mating. Other doves may be heard, but little or no attention is paid to them so long as they are not in sight. It was also found advisable to keep the mated pairs where they could not see other doves.

After a few days in the mating cages, a gentle shaking of the wings by both birds usually indicates that a mating has been accomplished, and the two may be placed in one cage with a nest. As males cannot be distinguished from females, with certainty, mistakes are often made in attempts at pairing. At such times, a pseudo-mating may result between males or between two females. Even copulation may take place, and only the appearance of two pairs of eggs or of no eggs at all after a reasonable period of waiting reveals the fact that the birds are not of opposite sex. Such birds readily take other mates when they are placed in cages as described above.

Fertile eggs may be laid in a few days after the birds are placed together. Thus on May 28, 1904, a pair of doves which had been kept in alternate cages for a few days were found to be amorously inclined. They were put in the same cage, and the first egg was laid on the 31st. This egg hatched about 8:30 A.M., June 15. The second egg was laid on June 2, and it hatched about 8:30 A.M., June 16. There was no reason to believe that the female had been fertilized by another male before the mating was begun. On June 23, the young doves were observed rising on their feet in the nest and elevating their wings. Their eyes were open on this date. These nestlings left the nest on the 27th, and one was observed sitting on a perch a few inches above the floor of the cage on June 28. Both were seen feeding from the seed dish used by their parents on the 30th. The plumage at this time was well developed except about the bill as is characteristic of young pigeons. The feathers of the bill region develop after the birds are weaned.

It was my experience that adult ring-doves more than one year old may begin breeding, when kept in a heated building,

in late January or early February. Breeding operations, even under apparently favorable conditions, may be delayed until May, especially with young birds. The greatest number of young produced in a season by a single pair of ring-doves was nine from five sets of two eggs each (see mating 8, Table XXI.). The records for this pair were as follows.

*Brood 1.*—First egg laid April 12, 1905. Hatched April 28.

Second egg laid April 14. Did not hatch.

*Brood 2.*—First egg laid May 15. Hatched May 31. Second egg laid May 17. Hatched May 31.

*Brood 3.*—First egg laid June 24. Hatched July 10. Second egg laid June 26. Hatched July 10.

*Brood 4.*—First egg laid Aug. 4. Hatched Aug. 20. Second egg laid Aug. 6. Hatched Aug. 21.

*Brood 5.*—First egg laid Oct. 5. Hatched Oct. 21. Second egg laid Oct. 7. Hatched Oct. 22.

With the first three broods, the eggs both hatched in the early morning of the fourteenth day after the second egg was laid. It will be noticed that there was some delay in the hatching of the eighth and tenth eggs as is apt to be the case at the end of the season. Both young of brood 4 died during the first week of September. Under favorable conditions, an average of six young per season may be considered good. Delays due to sickness, errors in mating, and occasional deaths reduce the average which might otherwise be higher. It will be seen in Table XXI. that there is a large variation in the number of eggs which are laid in a season.

The breeding habits of the blond ring-dove have been described by Whitman ('98), and in more detail by Craig ('08 and '09).

### III. RESULTS.

All of the hybrids which were obtained resembled one or the other of the parents. The dark hybrids had, however, a slight tendency to be somewhat lighter in color than the dark or blond parent. According to Professor Whitman, the voice of the hybrids tends to be intermediate. A comparison of the voices of many individuals is not easy to make, and I never felt certain enough about this point to venture an opinion one way or

the other. The white birds often show slight traces of melanin pigment in their feathers, but this was also observed in presumably pure stock as has been noted. The sex of ring-doves can be determined satisfactorily only by breeding tests or by dissection. The sex of a number of individuals was not ascertained as these died when there was no one on hand to make the necessary dissection. Some nestlings have also been included, and their sex was not determined.

The total number of hybrids hatched was 151, and the sex of 74 of these was ascertained. Of these, 32 were males and 42 were females. This preponderance of females is of no significance. Table I. gives results of crosses between blond males and white females. The ordinary Mendelian expectation is realized for color here, as all of the offspring in  $F_1$  are essentially like one parent in color, and the blond coloration is dominant. Whiteness of plumage or absence of pigmentation is recessive to the presence of pigment. Eight out of the ten birds of known sex were males.

TABLE I.

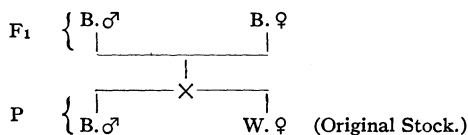
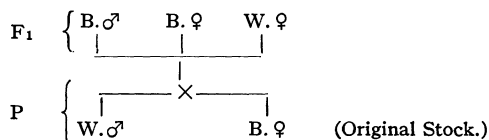
BLOND MALES  $\times$  WHITE FEMALES. MATINGS 1, 3, 4, 17, AND 23. $F_1$  14 offspring all dark. 8 males, 2 females, 4 sex ?.

TABLE II.

WHITE MALES  $\times$  BLOND FEMALES. MATINGS 2, 5, 16, 26, 29, 30, AND 33. $F_1$  18 blonds: 7 males, 3 females, and 8 sex?.

23 whites: 13 females and 10 sex ?.



With the reciprocal cross as in Table II., about one half of the offspring were white in  $F_1$ , and *all of the white birds whose sex was ascertained were females*. Again the dark hybrids were mostly males.

As only four blond female hybrids and no male white hybrids were obtained in  $F_1$ , it was not possible to do much breeding of hybrids *inter se*. Two pairs of blond hybrids were mated and the results of their breeding are given in Table III. The occurrence of a white bird in  $F_2$  is of course to be expected on a Mendelian basis. Again the same preponderance of males appears.

TABLE III.

BLOND  $F_1$  HYBRID MALES  $\times$  BLOND  $F_1$  HYBRID FEMALES. MATINGS 28 AND 44.

$F_2$  10 blonds: 3 males, 1 female, and 6 sex ?.

1 white female.

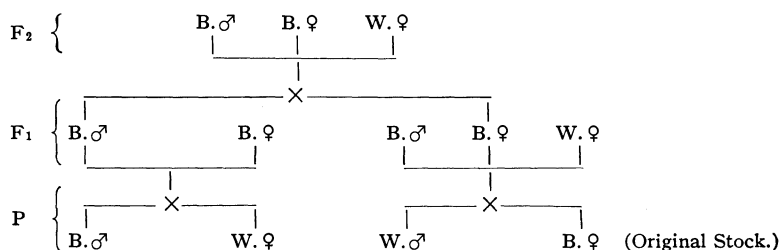


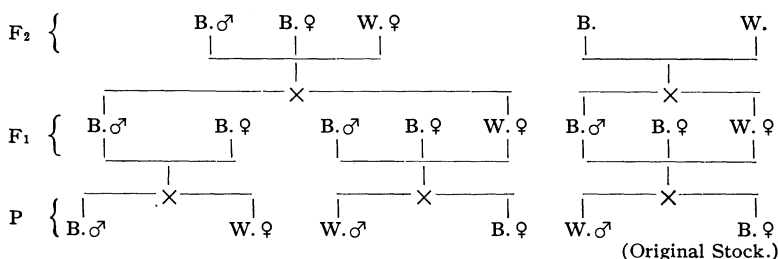
TABLE IV.

BLOND  $F_1$  HYBRID MALES  $\times$  WHITE  $F_1$  HYBRID FEMALES. MATINGS 14, 20, 35,

37, AND 42.

$F_2$  6 blonds: 1 male, 2 females, 3 sex ?.

5 whites: 3 females, 2 sex ?.



Blond hybrid  $F_1$  males when mated with white hybrid  $F_1$  females (see Table IV.) gave results which are similar to those obtained in Table II. where approximately equal numbers of white and blond birds occurred. Again the white birds sexed were all females.

Professor Whitman obtained similar results which were given to Bateson and are referred to by the latter in a footnote (Bateson,

'09, p. 194). Through the courtesy of Mrs. Whitman, I am permitted to give exact statistics as copied from Professor Whitman's records. These were known in a general way to me, having been discussed in conversations before his death, and they are as follows: when white male ring-doves were crossed with dark female ring-doves 5 blonds and 4 whites were obtained. White male ring-doves crossed with females of the very distinct species, *Turtur humilis*, produced five dark birds and twelve whites. In both crosses the white offspring were all females and the dark hybrids were all males "so far as was known."

There being no white  $F_1$  male hybrids, it was impossible to get  $F_2$  offspring from the white hybrids, and the white hybrids were consequently crossed back upon the original white stock (see Table VII.). All of the offspring of this cross were white, and males as well as females appeared. A white male was also obtained in a cross between a blond male and a white female both birds being the offspring of hybrids crossed back on the original stock (see Table XII.).

A blond hybrid male which had been obtained by crossing back was mated with a pure blond female, and all of the five offspring were blonds. Three of the four birds whose sex was learned were females. The effects upon the sex ratio of crossing back upon the original stock will be discussed later in this paper. Other results are given in Tables V., VI., VIII.-XI. and XIII.-XVII.

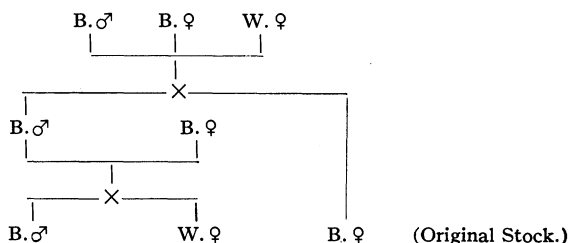
In looking over these results, it is quite apparent that white-

TABLE V.

BLOND  $F_1$  HYBRID MALE (TABLE I.)  $\times$  BLOND FEMALE. MATING 22.

Offspring 9 blonds: 5 males, 1 female, 3 sex ?.

5 whites: 4 females and 1 sex ?.



ness of plumage behaves as a sex-linked character in the crossings which are described in this paper. Associated with this whiteness are the pigmentation phenomena of the eye, and the scantier

TABLE VI.

WHITE MALE  $\times$  BLOND F<sub>1</sub> HYBRID FEMALE (TABLE I.). MATING 10.

Offspring 2 blonds: 1 male and 1 sex ?.

1 white: sex ?.

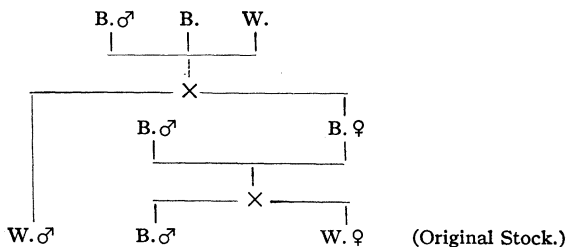


TABLE VII.

WHITE MALES  $\times$  WHITE F<sub>1</sub> HYBRID FEMALES (TABLE II.). MATINGS 8 AND 9.

Offspring 18 whites: 2 males, 3 females, 13 sex ?.

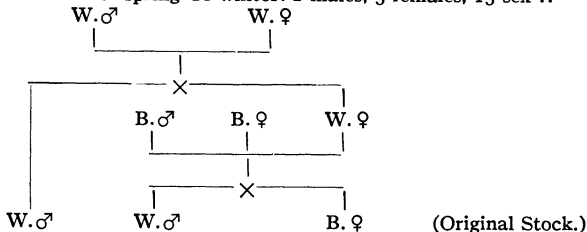


TABLE VIII.

BLOND MALE  $\times$  WHITE HYBRID FEMALE (TABLE V.). MATING 32.

Offspring 3 blonds: 2 males and 1 sex ?.

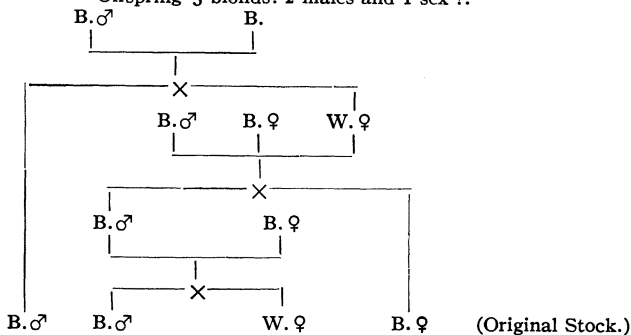


TABLE IX.

BLOND HYBRID MALE (TABLE V.)  $\times$  BLOND FEMALES. MATING 31.

Offspring 5 blonds: 1 male, 3 females, 1 sex ?.

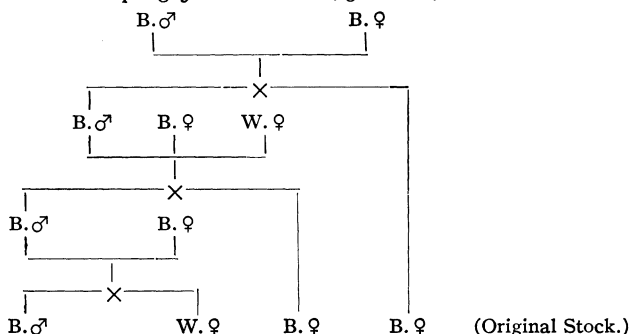
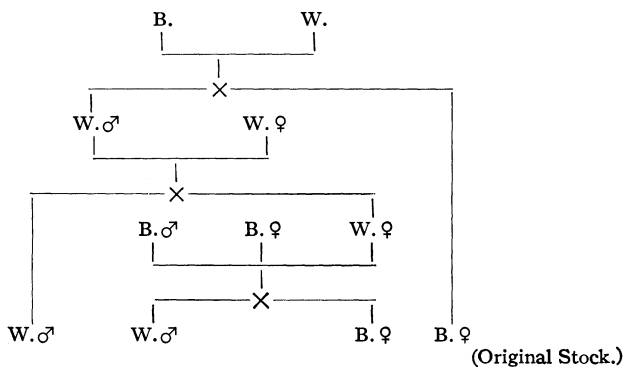


TABLE X.

WHITE HYBRID MALE (TABLE VII.)  $\times$  BLOND FEMALES. MATING 12.Offspring 6 blonds: sex ?.  
1 white: sex ?.

nestling down already described on pp. 296-8. These characters and doubtless others not noticed act as a group, and they appear in female birds of the  $F_1$  hybrid generation when the male bird possesses them. The characters of the blond bird come very near being sex-linked as they appear in only a few female hybrids.

There are many interesting points of resemblance between the results of these experiments and those obtained by some other workers. Apparently all of the cases of sex-linked inheritance in birds involve similar phenomena. Strikingly similar results

TABLE XI.

WHITE HYBRID MALE (TABLE VII.)  $\times$  WHITE HYBRID FEMALE (TABLE VII.).  
MATING 13.

Offspring: 3 whites: 1 female and 2 sex ?.

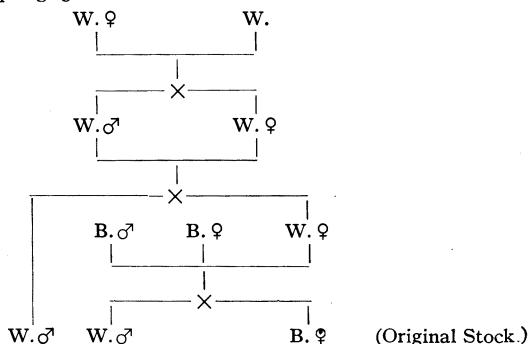
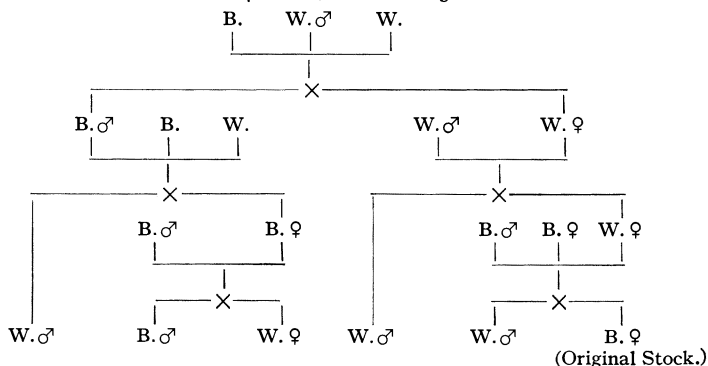


TABLE XII.

BLOND HYBRID MALE (TABLE VI.)  $\times$  WHITE HYBRID FEMALE (TABLE VII.).  
MATING 15.

Offspring: 2 blonds, sex ?.

4 whites, 1 male and 3 sex ?.



are those which were obtained by Durham and Marryat ('08) with canaries. Their cinnamon or pink-eyed canaries correspond in breeding behavior to the white ring-doves and their green or black-eyed canaries to the blond ring-doves. The results differ in that the ring-dove hybrids lack the variability which was characteristic of the canaries—a point of apparently no significance from the standpoint of the problems which are under discussion. No crossing comparable to their mating

TABLE XIII.

BLOND HYBRID MALES (TABLE I.) X WHITE HYBRID FEMALES  
(TABLE V.). MATINGS 39 AND 41.

Offspring: 6 blonds: 1 male, 3 females, 2 sex ?.

1 white female.

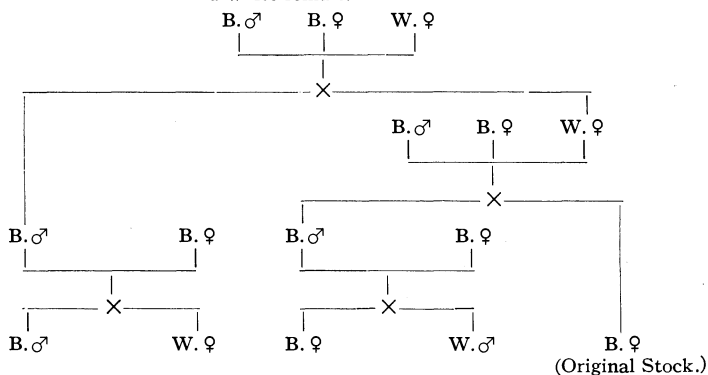


TABLE XIV.

BLOND HYBRID MALE (TABLE V.) X BLOND HYBRID FEMALE (TABLE I.).  
MATING 40.

Offspring: 2 blonds, sex ?.

TABLE XV.

BLOND HYBRID MALE (TABLE V.)  $\times$  WHITE HYBRID FEMALE (TABLE II.).  
MATING 43.

Offspring: 1 blond, sex ?.

TABLE XVI.

BLOND HYBRID MALE (TABLE I.)  $\times$  WHITE HYBRID FEMALE (TABLE XI).  
MATING 21.

Offspring: 2 blonds, sex ?.

TABLE XVII.

WHITE HYBRID MALE (TABLE XII.) X WHITE HYBRID FEMALE (TABLE VII.).  
MATING 10.

Offspring: 1 white female.

TABLE XVIII.

BLOND MALES  $\times$  BLOND FEMALES. MATINGS 24, 27, AND 38.

Offspring: All blond: 4 males, 5 females, 7 sex ?.

(Other matings of blond stock birds were made, and the offspring were also all blonds. They are not included here because exact records were not kept for them.)

## TABLE XIX.

WHITE MALE  $\times$  WHITE FEMALE. MATING 25.

Offspring: All white: 1 male, 3 white females, 3 sex ?.

No. 5 was attempted with the ring-doves because of a lack of white stock females. At the time the ring-dove matings were made, the work of Durham and Marryat was not known to the writer.

In all of the parallel cases (and these include some forms outside of the bird group), when the male parent has the dominant character, the offspring in  $F_1$  resemble the male parent and few or no females occur as a rule. When in the reciprocal cross the male bird is recessive, the offspring in  $F_1$  are about equally males and females; the recessive characters appear *only in female offspring*.

The sex-ratio for  $F_1$  offspring bearing the dominant characters varies greatly in different combinations. In both the canaries and the ring-doves the number of dominant females is very small and the proportion seems to be about the same in both. In some other combinations, as in the case of the crossings which were made by Pearl and Surface ('10a) between Barred Plymouth Rock males and Cornish Indian Game females, about equal numbers of males and females had the dominant barring. *No females* were barred in the reciprocal cross, however.

Other essentially similar cases are given in the following table where the dominant form is placed before the recessive. The famous experiments with currant moths described by Doncaster and Raynor ('06) could be included in this list if *laticolor* males occurred in nature.

## TABLE XX.

( $F_1$  females have dominant characters only when the male parent has them, in the following combinations:)

*Crossings.*

Brown Leghorn  $\times$  Silky fowl. Bateson ('09 and '11).

Black-red Game Bantam  $\times$  Brown-red Game Bantam. Hagedoorn ('09).

White Rock  $\times$  Brown Leghorn. Goodale ('10).

White Wyandotte  $\times$  Brown Leghorn. Sturtevant ('11).

Dark Brahma  $\times$  Brown Leghorn. Lacing characters. Davenport ('12).

Barred Rock  $\times$  Langshan, Morgan and Goodale ('12).

[In the above table I have classed the Silky fowl as recessive to the Brown Leghorn for the peculiar pigmentation which is characteristic of the Silky fowl mesodermal tissues. With this interpretation the case furnishes, in my judgment, a strong argument for the position taken in this paper as it does not seem probable that the pigmentation which appears in  $F_1$  females is derived from the Brown Leghorn hen.]

The commonly employed gametic analysis of these phenomena involves the assumption that in such cases, at least, the female is heterozygous for sex and the male homozygous. The female of the dominant form is assumed to be heterozygous also for the somatic characters involved. To various writers it has seemed more feasible to either ignore the opposing cytological evidence with regard to sex determination or to assume that the cytological conditions are different in these forms. Unfortunately, cytological evidence is difficult to obtain with birds, though Guyer ('09) has published observations which indicate that the common fowl has two kinds of sperms.

Other interpretations have been suggested by de Meijere ('11), who assumes that potentialities of both sexes are present in each gamete. According to de Meijere, one sex gets the upper hand in the egg during fertilization at the expense of the other. Just how this writer conceives of the operation in the phenomena of sex-linked inheritance, is not clear to me.

In thinking over these phenomena, I have been much impressed with the fact that *recessive characters appear in  $F_1$  only when the male parent is recessive*, and it is hard to resist forming the opinion that the recessive male is responsible for the situation. In the case of the turtle dove genus, whenever a white ring-dove male is crossed with a female blond ring-dove or with a female of *Turtur humilis*, white female offspring occur in  $F_1$ . As this paper is going to press, an article by Staples-Browne ('12) has appeared in which crossing experiments with pigeons are described. These include crosses between "Turtle doves" (*Turtur turtur*) and so-called "White Java Doves" which I infer

to be the white ring-doves of this paper. The results seem to be similar to those which were obtained by me, so far as they go. Two matings between "White Java" males and female "Turtle doves" were made and ten offspring were obtained—four "dark males," four "dark, sex uncertain" and two white females.

Staples-Browne also crossed the blond ring-dove (called "Barbary Dove" in his paper) with his "White Java" doves and obtained results which are like those described by me in this paper, except that in two matings between male blonds and white females, three male and three female white birds appeared in  $F_1$ . The explanation of these results given by Staples-Browne, that the male parents in these two cases were hybrids is undoubtedly correct. He states that much difficulty was experienced in obtaining pure "Barbary" stock.

Records are thus at hand of the appearance in  $F_1$  of white birds, whenever a white male ring-dove is crossed with females of at least two Linnæan species and also with the blond ring-dove. The assumption that the females of all of these three species, *Turtur risorius*, *T. humilis* and *T. turtur* are heterozygous for color seems to me more difficult to accept than the idea that the sperms of the male white ring-dove are responsible for the  $F_1$  white birds.

According to the interpretation of these cases of sex-linked inheritance which has been advanced by Spillman ('08), Bateson ('09) and others, the following two assumptions may be made in addition to those already stated (see Bateson, '09, p. 175): "That when in  $F_1$  the two dominant characters femaleness and the 'somatic' factor co-exist, there is spurious allelomorphism or repulsion between them, such that each gamete takes one or other of these factors, not both." The following scheme though familiar is repeated here for the sake of clearness in making a comparison with the interpretation which I am about to propose.

D = dominant. R = recessive.

1. Dominant ♂	×	Recessive ♀.
composition DD ♂♂		RR ♀♀
gametes all D ♂		R ♀
		R ♂

$F_1$ dominant males. DR ♂ ♂		dominant females. DR ♀ ♂
2. Recessive ♂ <i>composition</i> RR ♂ ♂ <i>gametes</i> all R ♂	×	Dominant ♀. DR ♀ ♂ R ♀ D ♂
$F_1$ dominant males. DR ♂ ♂		<i>recessive females.</i> RR ♀ ♂
3. Dominant $F_1$ ♂ <i>composition</i> DR ♂ ♂ <i>gametes</i> D ♂ R ♂	×	Recessive ♀. RR ♀ ♂ R ♀ R ♂
<i>dominant males.</i> <i>result</i> DR ♂ ♂ <i>recessive males.</i> RR ♂ ♂		<i>dominant females.</i> DR ♀ ♂ <i>recessive females.</i> RR ♀ ♂
4. Dominant $F_1$ ♂ <i>composition</i> DR ♂ ♂ D ♂ <i>gametes</i> R ♂	×	Dominant ♀. DR ♀ ♂ R ♀ D ♂
<i>dominant males.</i> <i>result</i> DD ♂ ♂ <i>and also</i> DR ♂ ♂		<i>dominant females.</i> DR ♀ ♂ <i>recessive females.</i> RR ♀ ♂

If, however, the female is regarded as homozygous for sex and also for somatic characters, and the male as heterozygous for sex, these phenomena may be explained in my judgment with the following additional assumption: that the female producing sperms of the recessive male have the power of suppressing or checking the development of dominant characteristics which may be carried by the egg or it may be that these sperms lack something which is necessary for the development of the dominant characters. This position is supported by all of the cytological evidence known to me, and it is not inconsistent with the idea that potentialities of both sexes may be present in both male and female gametes as well as in zygotes if such is the case. The castration experiments of Goodale ('10), for instance, have demonstrated that some female birds at least may develop male characteristics when

their ovaries are removed. The processes involved in determining the sex which dominates the organism may be the same whether one or both sexes are represented in it. So-called "spurious allelomorphism" is not assumed in this scheme.

This alternative interpretation may be applied to the ring-doves as follows. The female determining gamete is designated by the letter  $t$  as a subscript with an additional letter  $w$  in the case of the white male bird. All male gametes are designated by the male sign and female signs are used for the female gametes. These symbols are used thus with the hope that the formulæ may be more easily read, and also because it does not seem to the writer to be very appropriate to designate sperms, for instance, by both male and female signs as is commonly done when the male is regarded as heterozygous or to call eggs male and female as is done when the female is considered as heterozygous for sex. Both sexes are represented under the head of composition because the zygote is the result of a union of male and female gametes. Characters which are recessive to others in the same individual are included in parenthesis. In the case of  $F_1$  females, the  $w$  effect is interpreted as changing B to W.

- |   |           |                         |
|---|-----------|-------------------------|
| 1. Blond ring-dove male   | ×         | White ring-dove female. |
| <i>composition</i> B ♂ B (♀)                                      |           | W ♀ (W ♂)               |
| <i>producing gametes</i> { B ♂                                    |           | W ♀                     |
|   |           | W <sub>t</sub> ♀        |
| $F_1$ Blond males.  |           | Blond females.          |
| B ♂ (W ♀)   |           | B ♀ (W ♂)               |
| 2. White ring-dove male   | ×         | Blond ring-dove female. |
| <i>composition</i> W ♂ (W ♀)                                      |           | B ♀ B (♂)               |
| <i>producing gametes</i> { W ♂                                    |           | B ♀                     |
|   |           | B <sub>tw</sub> ♀       |
| $F_1$ Blond males, white females, and occasionally blond females. |           |                         |
| B ♂ (W ♀)   | W ♀ W (♂) | B ♀ (W ♂)               |

That the females in mating No. 2 are mostly white is explained by the assumption already made that the female determining gametes (subscript  $p$ ) of the male white bird are responsible for the absence of pigment. The  $w$  effect may or may not be connected with an accessory chromosome.

In the case of the canaries, Durham and Marryat found that their formula (*i. e.*, that given on pp. 310-1 of this paper) did not explain the occurrence of two  $F_1$  "black-eyed" females when the male bird was pink-eyed. The same difficulty appears with the ring-doves as may be seen on comparing Table II. where it will be seen that three blond  $F_1$  females appeared. The difficulty is no greater in the scheme just presented in this paper, and it would seem to be due possibly to the occasional failure of the  $_{tw}$  sperm to produce the  $_w$  effect.

It may be noted also that neither scheme explains the great excess of  $F_1$  males in the ring-dove and canary experiments. The occurrence of a preponderance of males is a common and well known result of crosses between bird species, for which no satisfactory explanation has been given. It is of course conceivable that female-determining sperms may in such cases encounter difficulties in the egg of another species which may be great enough to prevent the development of femaleness, more or less frequently. (See Guyer, '09a.)

The gametic analysis is carried still further as follows, and it may be noted that corresponding matings bear the same numbers.

3. Blond $F_1$ ring-dove male	×	White ring-dove female.
<i>composition</i> B ♂ (W ♀)		W ♀ W (♂)
B ♂		
$B_1$ ♂		
<i>producing gametes</i> W ♂		all W ♀
$W_{tw}$ ♂		
<i>result Blond males.</i>		<i>Blond females.</i>
B ♂ (W ♀)		B ♀ (W ♂)
<i>White males.</i>		<i>White females.</i>
W ♂ W (♀)		W ♀ W (♂)

See Table XII. of this paper where the birds crossed are probably potentially the same as the forms which are implied by this mating.)

4. Blond $F_1$ ring-dove male	×	Blond ring-dove female.
<i>composition</i> B ♂ (W ♀)		B ♀ B (♂)

	B ♂	
<i>producing gametes</i>	B <sub>f</sub> ♂	all B ♀
	W ♂	
	W <sub>tw</sub> ♂	
<i>result Blond males.</i>		<i>Blond females.</i>
B ♂ B (♀)		B ♀ B (♂)
and also		<i>white females.</i>
B ♂ (W ♀)		W ♀ W (♂)

(See Table V. of this paper.)

Still another mating combination is necessary to express the conditions which may be expected when F<sub>1</sub> blond ring-dove hybrids are mated *inter se* for the production of F<sub>2</sub> offspring.

5. Blond F <sub>1</sub> hybrid male	×	Blond F <sub>1</sub> hybrid female.
<i>composition</i> B ♂ (W ♀)		B ♂ (W ♀)
	B ♂	
<i>producing gametes</i> B <sub>f</sub> ♂		B ♀
	W ♂	W ♀
	W <sub>tw</sub> ♂	
<i>F<sub>2</sub> Blond males.</i>		<i>Blond females.</i>
B ♂ B (♀)		B ♀ B (♂)
and also		and also
B ♂ (W ♀)		B ♀ (W ♂)
White males.		White females.
W ♂ W (♀)		W ♀ W (♂)

(See Table III. of this paper.)

From the two matings of this sort made, only one, out of the eleven F<sub>2</sub> offspring obtained, was white, whereas the expectation would be one out of four. However, the number of F<sub>2</sub> offspring was too small to make a critical test and this result is not especially significant.

It will be observed that white hybrids crossed back on white stock and white hybrids crossed *inter se* (see Tables XI. and XVII.) gave white offspring, and males appeared as is to be expected. The white hybrids are so-called extracted recessives.

Other results were also obtained some of which have been mentioned on pp. 299-300 of this paper. In Table XXI., the following records may be found:

1. The number of broods in a season.
2. The number of eggs in a brood.

3. The eggs hatching.
4. The period of incubation for each egg, when known.
5. The sex and color of the nestling hatching from each egg.

TABLE XXI.

B., blond; W., white; K., died in egg; N. D., no development; ?, records uncertain.

Matings.	Brood 1.	Brood 2.	Brood 3.	Brood 4.	Brood 5.
(1904) 1	19B.; K.				
2	16W. ♀; 15W. ♀	K.; 16W.	Eggs small. N.D.; N.D.		
3	15B. ♀; 14B.				
4	N.D.; 14-B.	(August) 15-B.; 13-20B.	(September) N.D.; N.D.	(October) N.D.; N.D.	
5	16B. ♂; no 2d egg	16B. ♂; 14B.			
(1905) 8	16W.; K.	16W.; 14W. ♂	16W. ♀; 14-W.	16W.; 15W.	16W. ♀; 15W.
8	W.; W. March, 1906				
9	15W. ♂; 14W.	16W.; 14W.	14-12W. ♀; 14-W.	(November) 17W.; N.D.	
10	15B. ♂; 14B.	16W.; K.			
(1906) 12	16B.; 14B.	16B.; 15B.	K.; 14B.	15B.; 14W.	
13	N.D.; N.D.	15W. ♀; 14W.	?; ?		
14	16B.; N.D.	?; W.	?; ?		
15	15W.; 14W.	15W.; 14W. ♂	15B.; 14B.		
16	15B.; 14W.	15W.; 14.	?; ?	(October) N.D.; N.D.	(November) N.D.; N.D.
17	15B. ♂; 14B. ♂	15B. ♂; 14B. ♂	?; ?		
(1907) 19	16W. ♀; 14	15; K.	K.; K.		
20	K.; o	15B.; N.D.			
(1908) 22	W. ♀; W.	B. ♂; B. ♂	B. ♂; W. ♀	W. ♀; W. ♀	No breeding after June in 1907.
(1909) 22	15B. ♂; 14B.	B. ♂; o	14-B. ♀; 13-B. ♂	15B.; N.D.	
(1908) 23	B. ♂; N.D.	B. ♂; B. ♂	B. ♂; B. ♀		
24	B. ♀; B. ♀	B. ♀; B. ♂	B. ♀; B. ♂	B. ♀; B. ♂	
25	W.; W.	W. ♀; W. ♂	15W. ♀; 14W. ♀	W.; K.	
26	W. ♀; K.	W. ♀; W. ♀	15W. ♀; 14B. ♂		
(1909) 26	16B.; 16W. ♀	W. ♀; W.	16W.; 14W.	W.; W.	
27	N.D.; 14B. ♂	B.; o			
28	15B.; 14B.	16B.; K.	15B.; 14B. ♂	B. ♀; W. ♀	
29	26B.; 15B.	B. ♀; B.	15B. ♀; K.	15B. ♂; K.	
30	W.; W. ♀	15W.; 14B.	B. ♂; B. ♂		
31	B. ♀;	15B.; 14B. ♂	15B. ♀; B. ♀		
32	14B.; 13-B. ♂	15B. ♂; N.D.			
33	15W. ♀; B.	15W. ♀; 14W. ♀			
35	15W. ♀; 14B. ♀	15B.; 14W.			
37	15B. ♀; 14B. ♂				
38	15B.; 14B.	16B.; 14B.	15B.; 14B.		
39	15B. ♀; o	15B. ♀; 14B. ♀			
40	15B.; 14B.				
41	15B. ♂; 14	W. ♀; B.			
42	15W. ♀; 14W. ♀				
43	B.; N.D.				
44	B. ♂; B.	15B. ♂; 15B.			

In the above table the period between laying and hatching is given, when known. In some cases, as in mating 4, brood 2, this period is indicated in both days and hours. When no second egg was laid, a zero appears. Both birds were stock blonds in matings 24, 27, and 38. Stock whites were used in mating 25.

TABLE XXII.

Matings.	See Table.	Total Eggs Laid.	Total Eggs Hatched.	Total Offspring.					
				Blond.			White.		
				♂ ♂	♀ ♀	Sex ?	♂ ♂	♀ ♀	Sex ?
1	I.	2	1						
2	II.	6	3					2	1
3	I.	2	2		I	I			
4	I.	8	3			3			
5	II.	3	3	2		I			
8	VII.	10	9				I	2	7
8	VII.	2	2						2
(1906)									
9	VII.	8	7				I	I	4
10	VI.	4	3	I		I			I
12	X.	8	7			6			I
13	XI.	6	3					I	2
14	IV.	6	4			I			I
15	XII.	6	6			2	I		3
16	II.	10	6	I		I		I	2
17	I.	6	6	4					
19	XVII.	6	3			I		I	
20	IV.	3	1			I			
21	XVI.	2	2			2			
22	V.	8	8	3	5			4	I
22	V.	8	6	3	I	2			
(1909)									
23	I.	4	4	4	I				
24	XVIII.	8	8	3	5				
25	XIX.	8	7				I	3	3
26	II.	8	5	I				4	
26	II.	8	8			I		2	5
(1909)									
27	XVIII.	5	2	I		I			
28	III.	8	7	I	I	4			
29	II.	8	6	I	2	3			
30	II.	6	6	2		I		I	2
31	IX.	5	5	I	3	I			
32	VIII.	4	3	2		I			
33	II.	4				I		3	
35	IV.	4	4		I	I		I	I
37	IV.	2	2	I	I				
38	XVIII.	6	6			6			
39	XIII.	3	3		3				
40	XIV.	2	2			2			
41	XIII.	4	4	I		2		I	
42	IV.	2	2					2	
43	XV.	2	1			I			
44	III.	4	4	2		2			
Totals		218	174	34	19	48	4	30	36

As the first egg laid was regularly marked, it was possible to know which egg hatched first. In Table XXI., the first egg laid appears before the other. The first nestling to hatch was marked by a clipped toe. Aluminum ring-band tags were placed on one leg of each bird before it left the nest.

Some of these data are given in other form in Table XXII. where each mating is referred to the table which describes it.

The periods between laying and hatching may be summarized as follows in Table XXIII.

TABLE XXIII.

	Period.	Stock.	Number of Individuals.	
			Blond Hybrids.	White Hybrids.
First egg.	15 days.	5	26	12
" "	16 "	2	8	9
" "	17 "			1
" "	19 "		1	
Second egg.	14 days.	5	22	14
" "	15 "		3	3
" "	16 "			
" "	18 "			

It will be noticed that no cases of more than two eggs in a clutch occurred.

The idea has existed that the first eggs in a pigeon clutch usually give rise to males, though I know of no studies which would support this idea. An inspection of the data in Table XXI. proves this assumption to be without foundation with ring-doves at least. A summary of the results from those matings where the offspring were not mostly either males or females is given below. The matings from which the statistics were taken are as follows: Nos. 2, 8-10, 15, 16, 22, 24-33, 35, 37-40, 42 and 44.

First egg.....	Male	13
" ".....	Female	28
Second egg.....	Male	15
" ".....	Female	15

It is obvious that ring-doves, at least, do not show any correlation between sex and the order of laying or of hatching. Cole ('11) obtained similar results with tumbler pigeons.

#### IV. SUMMARY.

1. Hybrids between blond male ring-doves and white female ring-doves are all blonds and they are mostly males.

2. The offspring of the reciprocal cross are about equally blonds or whites, but *all of the white birds are females*. Whiteness and the characters associated with it are sex-linked. Al-

most all of the blond birds are males. Male white birds appear, however, when white hybrid females are crossed back on white stock males.

3. The nestling hybrids are identical in appearance with the nestlings of the corresponding blond and white uncrossed ring-doves.

4. The phenomena observed are remarkably similar to those described by Durham and Marryat ('08) for canaries.

5. Sex-linked inheritance in birds and elsewhere also can be explained, in my judgment, more logically with the assumption that the male is heterozygous for sex and the female homozygous, than by the contrary hypothesis.

6. The appearance of recessive characters in  $F_1$  when the male parent is recessive may be explained with the assumption that the female determining gametes of the male parent may either possess or lack something which is responsible for the absence in female offspring of dominant characters carried by the female parent.

7. No evidence was obtained in support of the old idea that the first egg laid by doves produces a male.

8. Observations concerning the period of incubation and other points in the breeding habits of ring-doves are described.

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